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## **The staggered marsupial third lower incisor: hallmark of cohort Didelphimorphia, and description of a new genus and species with staggered i<sub>3</sub> from the Albian (Lower Cretaceous) of Texas**

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**Abstract.** Progressive reduction in length of evolving marsupial muzzle incurred dental crowding and loss. Disappearance of the first lower incisors in earliest marsupials was followed by suppression and loss of first molars, the so-called “milk premolars”, possibly in earliest Cretaceous or latest Jurassic. Crowding and staggering of the lower third incisor which occurred not later than early Cretaceous, became the hallmark of Cohort Didelphimorphia. The phylogenetic and biogeographic significance of staggered i<sub>3</sub> (numerical second) usually supported buccally by a bony buttress, are discussed. Dental formulae of Metatheria and Eutheria are compared and shown to be developmentally and serially non-homologous. The new genus and species from the Texas Albian (upper Lower Cretaceous) described here may be the oldest didelphoid known. Its staggered i<sub>3</sub> implies an Early Cretaceous or Late Jurassic time of Metatherian differentiation.

**Key words.** Metatheria, Eutheria, dental formulae, evolution, Marmosidae, new genus, new species, Cretaceous, Texas.

### **Introduction**

The primitive number of upper and lower incisors in the ancestral marsupial was five. Reduction in mandibular length incurred loss of first lower incisor (Winge 1893, 1941; Woodward 1893, 1896; Berkovitz 1978). The second lower incisor, now the numerical first, is normally developed and functional as are the third and fourth and, where still present, the phylogenetic fifth or numerical fourth. The phylogenetic third lower incisor (i<sub>3</sub>) or numerical second, is likewise normal with respect to form and approximate size of crown. In the didelphimorphs, however, the root of i<sub>3</sub>, because of reduction of alveolar space, is wedged between the roots of adjacent teeth.

The staggered position caused by crowding seems to have given rise on the buccal side of the root to a bony process or buttress that may project above the alveolar line of the adjacent teeth (fig. 1). No other incisor or its alveolus is so marked and no other tooth in the same jaw can be confused with it. Its persistence in a field where one or more teeth have already been eliminated testifies to the identity of this complex within the Cohort Didelphimorphia. Marsupial classification and terminology used here follow Hershkovitz (1992).

A staggered i<sub>3</sub>, or its alveolus, the numerical second of the functional lower incisor series ([1], 2, 3, 4, 5), is the hallmark of all living didelphoids and all fossil didelphoids known to me with lower incisors or alveoli intact (fig. 2). A possible exception has been noted, however, assuming correct identification as a “didelphid” or didelphoid. As described by Fox (1983, p. 1572), the i<sub>3</sub> of a specimen he referred to

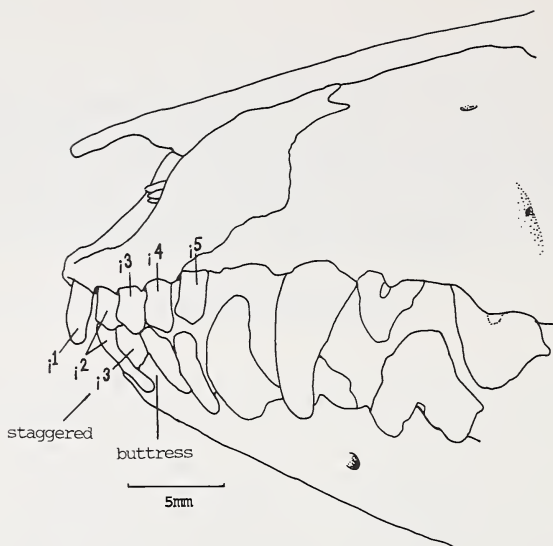
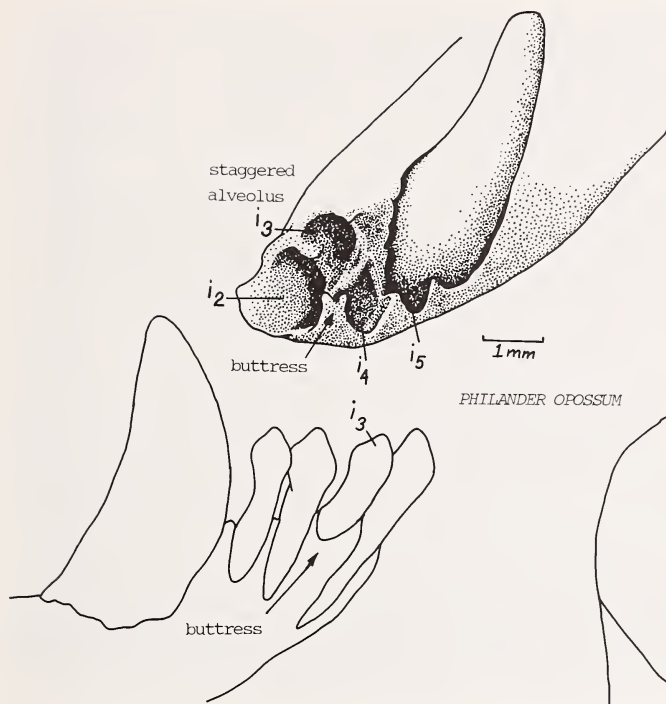


Fig. 1: Incisors of the common Neotropical opossum *Didelphis marsupialis* in normal occlusion. Arrow points to bony buttress of staggered  $i_3$  (South America). Redrawn from Hershkovitz (1982).

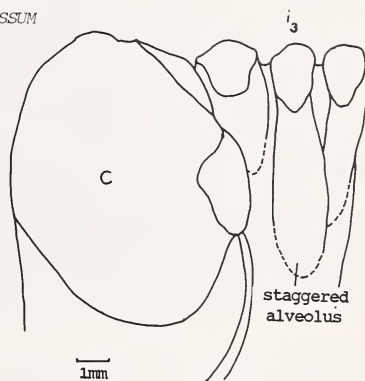
*Herpetotherium fugax* Cope, from the White River Formation (Middle Oligocene) appears to be unstaggered. As figured (Fox 1983, pp. 1568, 1569), the large size and slightly mediad rotation of the tooth may be suggestive of the staggered condition but it and the other lower incisors appear well separated from the others and are not supportive of such interpretation. Relative size, proportions and spacing of each incisor do not resemble any previously described incisor suite known to me. The same appears to be true of the relative size and spacing between the premolars of the fossil. The anteroposterior alveolar length of the two-rooted first upper premolar, as figured, is about as long as the figured alveolar length of the second premolar and longer than the third. The characters shown are not present in any other described marsupial seen by me.

A marsupial mandibular symphysis with intact incisors or alveoli is rarely found fossil. Many of those with staggered  $i_3$  described or figured in the literature or preserved in the Field Museum are noted below. A specimen at hand of *Peratherium* sp. (FM PM-1011) with lower incisors complete, clearly exhibits the staggered  $i_3$ . The  $i_3$  of *Peratherium perrierense* figured by Archer (1984, p. 619, fig. 59) also appears to be staggered. As illustrated by Storch & Haubold (1989, p. 98, fig. 1) the  $i_3$  of the Geiseltal, Germany, Middle Eocene *Amphiperatherium* aff. *maximus* Crochet, 1979, may be staggered, whereas that of their (1989, p. 104, fig. 5) *Peratherium* aff. *monspeliense* Crochet, of the same fauna, is clearly staggered.

The Late Paleocene *Peradectes elegans* Matthew & Granger (Peradectidae) figured by Fox (1983, p. 1575) shows the staggered  $i_3$ . The unmistakable didelphoid is treated as an Order of a new Cohort "Alphadelphia" by Marshall et al. (1990, p. 458). The



PHILANDER OPOSSUM



BORHYAENA MACRODONTA

Fig. 2: A. Bottom, incisors and canine of four-eyed pouched opossum *Philander opossum* (Didelphidae). Top, exposed alveoli reveal staggered position of  $i_3$  between  $i_2$ -4 (South America). Redrawn from Hershkovitz (1982).

Fig. 3: Extinct borhyaena *Borhyaena macrodonta*; lingual aspect of left ramus with incisors and canine (Colhue Huapí, Chubut Argentina). Redrawn from Hershkovitz (1982).

wedged  $i_3$  is also apparent in the Eocene *Prepidolops didelphoides* Pascual (Prepidolopidae Pascual, 1980, fig. p. 222). It is present in the borhyaenids *Borhyaena macrodonta* Ameghino, L. Oligocene (FM P 13252) (fig. 3), *Sipalocyon gracilis* Ameghino, L. Oligocene (Princeton Univ. PU 153373) (fig. 4), the Oligocene *Arctodictis sinclairi* Marshall (Marshall 1976, fig. p. 54) and the Recent Tasmanian Wolf (*Thylacinus cynocephalus*) (fig. 5). It is described and figured in the stagodontid *Eodelphis browni* Matthew, Late Cretaceous (Matthew 1916, p. 482, pl. 2, fig. 1). The staggered  $i_3$  alveolus of the late Early Cretaceous (Albian) edentulous mandible was figured by Hershkovitz (1982, fig. 5).

In his report on the Santa Cruz marsupials of the Patagonian early Miocene, Sinclair (1906) saw that the numerical second lower incisors ( $i_3$ ) of the borhyaenoids and caenolestids were staggered. Genera represented were *Prothylocinus*, *Cladosictis*,

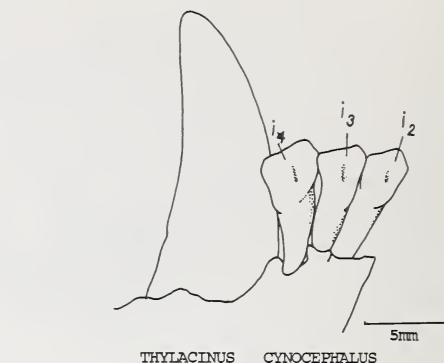
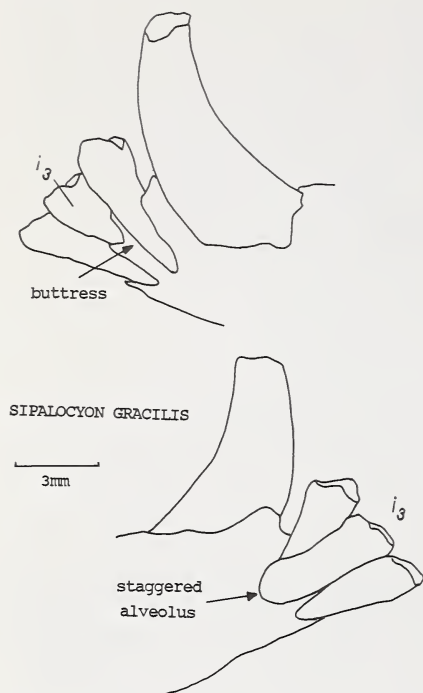


Fig. 5: Tasmanian wolf, *Thylacinus cynocephalus* (Thylacinidae). Right ramus with incisors and canine (Tasmania). Redrawn from Hershkovitz (1982).

Fig. 4 (left): Extinct borhyaena, *Sipalocyon gracilis*. Left ramus with incisors and canine: Top, labial view; bottom, lingual view (Santacrucian, Argentina). Redrawn from Hershkovitz (1982).

*Amphiproviverra* (*Sipalocyon*), and the caenolestid *Halmarhiphus*. As described by Sinclair (1906, p. 348, pls 40, 45, fig. 3) the lower incisors of the *Borhyaena* "are closely crowded and the root of the second [ $i_2$ ] is displaced posteriorly with reference to the median and lateral teeth, as in *Thylacinus* (fig. 4) and the Santa Cruz genera [of marsupials] in general." Excluded were the Microbiotheriidae. Their lower incisors, Sinclair (1906, p. 409) noted, are "spatulate in shape, resembling the incisors of *Dasyurus* rather than *Didelphis*. Unlike these genera the root of the second tooth [ $i_2$ ] in the series is not displaced posteriorly with reference to the roots of the first and third (fig. 5)." See also Hershkovitz (1992).

Morphological conditions for persistence of a staggered  $i_2$  have disappeared in the extinct South American Groberiidae and Argyrolagidae. The status of  $i_2$  in other extinct American marsupials (Carolameghiniidae, Polydolopidae, and Patagoniidae) is unknown.

Staggered  $i_2$  in Australian marsupials. Australian polyprotodont marsupials have lost an additional lower incisor, but the staggered  $i_2$  persists nonetheless in most. The incisor formula is 4/3 in the Dasyuridae (fig. 6), Thylacinidae (Order Dasyuromorphia, Marshall et al. 1990), all with staggered  $i_2$ . The incisor formula is 5/3 in the Peramelidae, Thylacomyidae and Notoryctidae (Order Peramelina, Marshall et al. 1990). In these, and the Myrmecobiidae, mandibular elongation coupled with attenuation tends to eliminate or reduce dental crowding and staggering in the

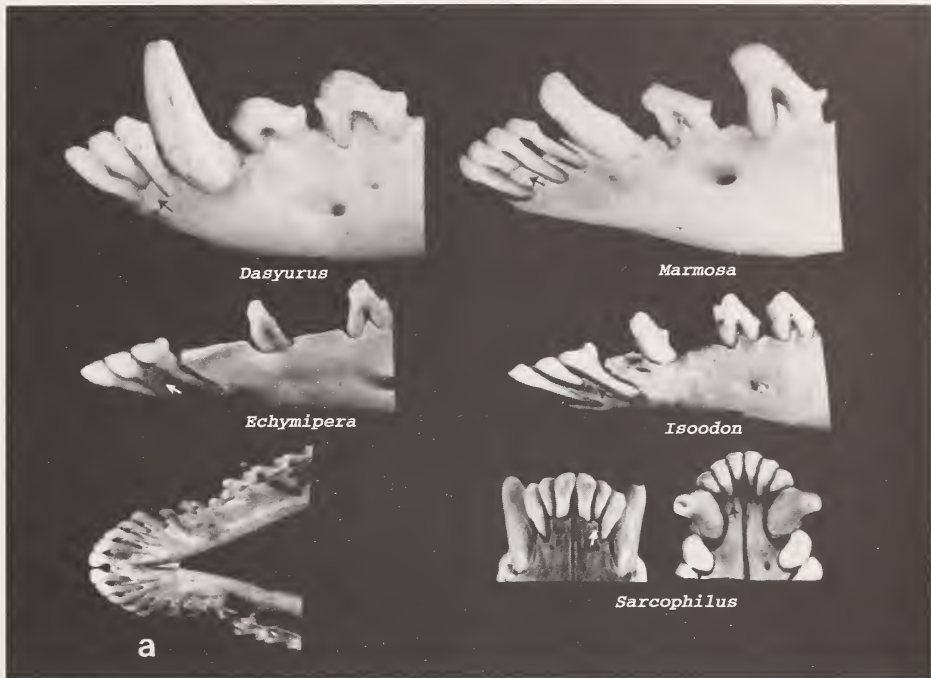


Fig. 6: Staggered  $i_3$  and buttress in Australian marsupials, labial aspects; (*Dasyurus*, *Echymipera*, *Isoodon* and *Sarcophilus*, labial and lingual aspects); top right, American *Marmosa*. Bottom left a, *Dromiciops gliroides* with nonstaggered, nonbuttressed  $i_3$ . Modified from Hershkovitz (1992).

incisor field. Nevertheless,  $i_3$  remains staggered in all specimens of *Perameles*, *Isoodon* and *Echymipera* (fig. 6) in the Field Museum collection, other peramelids not represented.

**Homologies.** In the Order Dasyuromorphia, the first upper incisor appears to be comparable to the didelphoid first upper, hence serially homologous. The numerical first lower incisor ( $i_2$ ) occludes with the second upper as in didelphoids. The numerical second lower incisor or phylogenetic  $i_3$ , is staggered and buttressed and cannot be other than the homologue of the staggered didelphoid  $i_3$ . The third lower incisor (numerical fourth) crowded by the canine, appears normal, but alveolar space for an additional incisor is not evident. A vestigial fourth lower incisor, the putative  $i_5$ , however, occurs in a specimen examined of *Myrmecobius fasciatus* (FM 35259). The extended incisor formula of the Dasyuromorphia, calculated from the position of staggered  $i_3$ , and occlusion between apparent serially homologous upper and lower teeth is,  $\frac{1, 2, 3, 4, (5)}{(1), 2, 3, 4, (5)} = \frac{4}{3}$ , and in the Peramelina,  $\frac{1, 2, 3, 4, (5)}{(1), 2, 3, 4, (5)} = \frac{4}{3}$ , the missing teeth shown in parentheses.

Remarks. Mandibular modifications with the effect of eliminating  $i_3$  crowding take on various forms. In ant-eating Myrmecobiidae, for example, the three lower incisors are widely spaced in the elongate jaw. In Australian diprotodonts with uncrowded incisors, the lower medial pair of incisors are greatly enlarged, the others reduced in size and number, or absent. As shown by Woodward (1893), the hypertrophied first lower incisor of wallabies (and all other Australian diprotodonts) are homologous with the second or phylogenetic  $i_3$  of polyprotodonts (fig. 7).

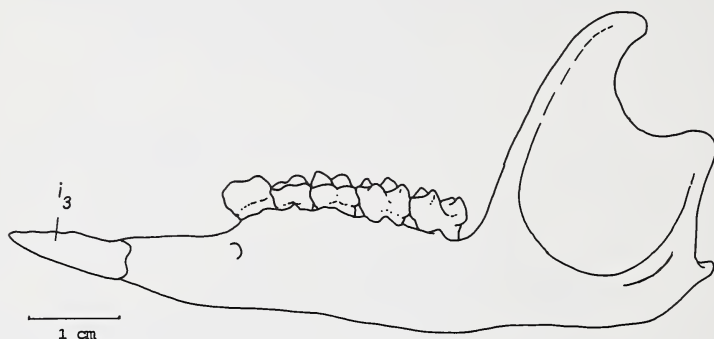


Fig. 7: Rock wallaby *Petrogale inornata* (Macropodidae), left ramus with staggered  $i_3$  (Queensland, Australia). Redrawn from Hershkovitz (1982).

Caenolestidae (*Caenolestes*, *Lestoros*, *Rhyncholestes*): Elongation of the upper jaw in caenolestids was not accompanied by an equivalent prolongation of the mandible. Instead, the gap between the jaws was bridged by elongation of the lance-like first-in-line incisor or phylogenetic  $i_2$ . Reduction to near obsolescence of the remaining antemolar teeth decreased incisor tooth crowding in caenolestids but phylogenetic  $i_3$  remains pinched between the adjacent incisors. Front teeth reduction in *Rhyncholestes* is more derived, but  $i_3$  staggers over  $i_2$ .

Microbiotheriidae. In *Dromiciops* (figs 6a, 8), the lone surviving taxon of the family and Cohort Microbiotheriomorpha, the spatulate crowns of lower incisors touch, sometimes with slight overlap but without stagger. Mandibles of the holotypes of Miocene *Microbiotherium tontor* and *M. tehuelchum* lack at least the

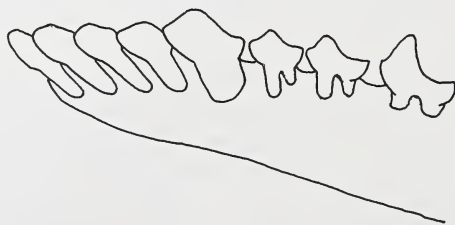


Fig. 8: Monito del monte, *Dromiciops gliroides*. Labial aspect,  $i_3$  not staggered, not buttressed.

front two incisors but the orientation of  $i_{2-5}$  alveoli present in *M. tehuelchum*, agree with those of *Dromiciops*. The small canine contrasted with the comparatively enormous canine of the Albian didelphid PM 258, or of didelphoids generally, is attributed to retention of the normal or primitive interdental relationships.

The Microbiotheriomorphia, of indisputable, South American origin was inadvertently indicated by Hershkovitz (1992, p. 206) as North American.

### Metatherian and eutherian lower incisors compared

The permanent lower incisors of adult eutherians are normally replacement or second generation teeth. They are neither serially nor individually homologous with the equivalent unreplaced or first generation lower incisors of metatherians. The same is true of upper incisors, upper and lower canines, and premolars. Only the unreplaced or first generation eutherian molars are comparable but not demonstrably numerically homologous with first generation metatherian molars. Neither clade can be derived from the other nor are they divergent from a common ancestor.

The basic number of first and second generation eutherian incisors is  $\frac{3}{3}$ , expressed as  $\frac{1, 2, 3}{1, 2, 3}$ . The count is often much higher in toothed whales (suborder Odontoceti, order Cetacea) and some insectivores (order Insectivora) including a few species of living shrews (family Soricidae), and possibly late Cretaceous forms of Palaeoryctidae. Except in multitoothed whales, and, paradoxically, some edentates, the evolutionary trend has been towards loss of teeth. In some metatherians, the number of functional incisors has been reduced to  $\frac{1}{1}$ , in some eutherians, all have disappeared.

True homology between first generation eutherian and metatherian lower incisors, and between second generation eutherian and first generation metatherian lower incisors is unlikely (cf. Kirkpatrick 1978, p. 34). Nevertheless, interrelationships between adult or second generation lower incisors of certain eutherians parallels that of first generation metatherian lower incisors.

Among Carnivora, a staggered  $i_2$  in a crowded  $\frac{3}{3}$  incisor field is the usual condition in Ursidae, common in Mustelidae, Viverridae, Hyaenidae, individually variable in Canidae and Procyonidae, and uncommon in Felidae except *Acinonyx*. A staggered  $i_2$  is probably similarly distributed among extinct Carnivora but fossil jaws with fully toothed mandibular symphyses are poorly represented in the Field Museum collections. Only a single carnivore with staggered  $i_2$ , that of the Miocene *Aleurodon* (Canidae) was preserved. A staggered  $i_2$  of the Eocene *Vulpanus profectus* (Miacidae) is figured by Matthew (1909, p. 383, fig. 23). In all Carnivora examined,  $i_2$  is consistently larger than  $i_1$  and smaller than  $i_3$ .

Staggered  $i_2$  has not been seen in other kinds of living or extinct eutherians represented in the Field Museum collections or described or figured in the literature consulted. There are, however, many instances of incisor crowding and crown overlap among the Insectivora with 3 lower incisors on each side but no clear evidence of root or alveolar staggering. In some insectivores with 2 lower incisors such as hedgehogs (Erinaceidae), the missing  $i_1$  may have been crowded out by the enlarged,

recumbent and possibly staggered  $i_2$ ; the greatly reduced  $i_3$ , compressed between the hypertrophied  $i_2$  and canine also appears to be in process of disappearance. Lower incisors in Chiroptera with primitive dentition are also often crowded with crown overlap frequent but I find no instance of staggering in any Field Museum specimen. The chiropteran  $i_2$  is not larger than other incisors and not always the remaining tooth in an incisor field reduced to 1 (Miller 1907, p. 25).

Comparisons between adult metatherian and eutherian lower incisors are summarized as follows, teeth lost in embryogenesis or phylogeny enclosed in parentheses.

#### Metatheria

1. Functional young or adult incisors are unreplaced or first generation teeth. Potential successional teeth may have been suppressed during embryogenesis.
2. Primitive functional first generation lower incisor formula is (1), 2, 3, 4, 5, in the earliest metatherian known.
3. Complete mandibular dental field formula is  $i\ 4$  (5);  $c\ 1$ ;  $pm\ 3$ ;  $m\ 4$  (5). For loss of first molar see Archer (1978) and Hershkovitz (1982).
4. The adult staggered lower incisor (or alveolus) in polyprotodonts with 3 or more lower incisors is the midfield first generation  $i_3$ ; a raised alveolar buccal buttress is normally present.
5. Staggered condition of first generation  $i_3$  (or alveolus) is plesiomorphic for all didelphoids including the Australian forms.
6. Secondary loss of staggered condition of first generation  $i_3$  in Australian didelphoids may be result of (a) loss of one or both contiguous incisors, (b) reduction in canine size, (c) ontogenetic loss of first molar, (d) mandibular elongation.
7. First generation  $i_3$  often largest incisor and normally not lost (but in caenolestids smaller than the lanceolate  $i_2$ ).
8. First appearance of staggered  $i_3$  in metatherians identifies the Didelphimorphia.

#### Eutheria

1. Functional adult incisors are successional second generation teeth; they replace functional first generation deciduous or "milk" teeth.
2. Basic second generation lower incisor formula is 1, 2, 3; that it may have been 1, 2, 3, (4), or (1), 2, 3, 4, or 1, 2, 3, 4, is unlikely.
3. Complete mandibular dental field formula is  $i\ 4$ ;  $c\ 1$ ;  $pm\ 4$ ;  $m\ 3$ . Whatever the formula, second generation incisors are neither individually nor serially homologous with first generation marsupial incisors.
4. An adult "staggered incisor" (or alveolus) if present, is midfield second generation  $i_2$ , buttress not usually present.
5. "Staggered" condition of second generation  $i_2$  is derived or secondary. It developed independently in certain lines of Ferungulata (sensu Simpson, 1945); staggered or not, neither  $i_2$  nor  $i_3$  is homologous with the marsupial  $i_3$ .
6. Unstaggered second generation  $i_2$  is primitive or ancestral and persists in most eutherians with 3 lower incisors.
7. Second generation  $i_2$  usually equal to or smaller than second generation  $i_3$  and is last or penultimate incisor to erupt in some phyletic lines.
8. First appearance in therians of one or more functional second generation teeth derived from first generation incisor formula  $\frac{1, 2, 3}{1, 2, 3}$  (or as in item 2 above), defines earliest eutherian dental grade.

Remarks. Items 5 through 8 cannot be truly compared or equalled for lack of homologous elements. The differences itemized indicate that metatherian and eutherian dental systems evolved independently each from a different base. For a masterful analysis of the independence of the two clades and a retreat from convictions, see Lillegraven (1969).

### Phylogenetic and biogeographic significance of the staggered $i_3$

The staggered  $i_3$ , a derived character, is a didelphoid autapomorphy that stamps all living and extinct forms even those where secondarily lost. Included are the Prepidolopidae, Borhyaenidae, Stagodontidae, Peradectidae, Caenolestidae, all polyprotodont marsupials with at least the first to third numerical lower incisors in place, and Australian diprotodonts with  $i_3$  persistent.

In Australian polyprotodonts with all but a single pair of incisors that pair is taken for the original  $i_3$  (Woodward 1893). Marshall et al. (1990, p. 1466) list 11 families among the 44 living and extinct Australian and American marsupials with a single pair of incisors.

The staggered  $i_3$  (or alveolus) present in American and Australian marsupials implies that the dental feature was common before Australian marsupials separated from their South American ancestors. It is highly unlikely that this seemingly anomalous character would have arisen independently in virtually identical form on both continents. Presence of a staggered  $i_3$  alveolus in the mandibular fragment of the Early Cretaceous North American didelphoid PM 583 not only confirms the antiquity of the character complex and its homology in descendants but marks or defines didelphoid differentiation from a primitive unstaggered condition such as in microbiotheriids.

### Earliest staggered $i_3$ and oldest didelphoid (fig. 9)

The edentulous mandibular fragment with the staggered alveolus of  $i_3$ , recovered in the Trinity Sands of Albian age, late Early Cretaceous, and registered PM 583 in the collections of the Field Museum, is hardly distinguishable from the same part of a young living *Marmosa murina* Linnaeus the stagger included (fig. 6). It had been classified by previous investigators as therian of "metatherian-eutherian" grade, the staggered alveolus of the missing tooth unnoticed. So it remained since first described by Patterson (1956). Reexamination of the mandible by Hershkovitz (1982) revealed the dental trait as unique to all known didelphimorphs. The staggered condition of  $i_3$  continued to be ignored nonetheless by later workers until Creighton noted in his unpublished doctoral dissertation (submitted 1984), that "Hershkovitz (1982) has surveyed the distribution of this seemingly trivial character in extinct and recent marsupials of the eastern and western hemispheres. The staggered and buttressed  $i^3$  [sic =  $i_3$ ] is present in most recent and extinct polyprotodont marsupials and all didelphids, but is not developed in *Dromiciops* or any of the known fossil microbiotheriids. Based on the nearly ubiquitous presence of this trait in fossil and recent didelphids and their presumed relatives (e. g. borhyaenids) it seems best to regard the lack of a buttressed  $i_3$  as a specialized feature, unique (among this study

collection) to *Dromiciops*." On the contrary, the buttressed  $i_3$  is obviously derived and the unbuttressed  $i_3$  is the natural or primitive character retained in the Microbiotheriidae, *Dromiciops* included (cf. Hershkovitz 1992).

*Pappotherium* and *Holoclemensia*. The Albian PM 583, described below, may not be the first known Early Cretaceous fossil with didelphoid credentials. A right maxillary fragment with last two molars recovered from another site near the same Albian Paluxy Formation that yielded the mandible, were described by Slaughter (1965) as *Pappotherium pattersonii*. The *Marmosa*-size tritubercular molars could be those of a eutherian ( $m^{2-3}$ ) or a metatherian ( $m^{4-5}$ ). Associated premolars appeared more likely eutherian. The lot were treated as therians of "eutherian-metatherian" grade. Shortly thereafter, Slaughter (1968a) recovered from another site of the same locality an upper marmosid-size molar with protocone missing. It was described as a didelphid and named *Clemensia texana*. An isolated last upper molar was designated paratype and a lower molar was referred. Because of homonymy with an earlier named lepidopteran, Slaughter (1968b) replaced the name *Clemensia* with *Holoclemensia*. Later, Slaughter (1971) redefined *Pappotherium* as eutherian very near to if not a form of Insectivora. The status of *Holoclemensia* as didelphid was maintained.

Treatment of *Pappotherium* as eutherian and *Holoclemensia* as metatherian was not generally accepted. According to Clemens (1966; 1968) and Lillegraven (1969) both genera were better regarded as theria of "eutherian-metatherian" grade. The judgement was accepted by Turnbull (1971), Tedford (1974), Clemens again (1977), Crompton & Kielan-Jaworowska (1978), Clemens, Lillegraven, Lindsey & Simpson (1979), Kielan-Jaworowska, Eaton & Bown (1979 and figures p. 188), and Clemens still again (1979). At another time Clemens (1971a; 1971b), and Lillegraven (1974) followed Slaughter's (1971) treatment of *Holoclemensia* as marsupial. Fox (1980, p. 1497) did in fact regard *Holoclemensia* as a marsupial and *Pappotherium* as a member of the eutherian order Insectivora. Hoffstetter (1975) thought both taxa might be marsupials but concluded that neither had evolved beyond "eutherian-metatherian" grade. A detailed reexamination of the original Patterson and Slaughter material convinced Butler (1978) that *Pappotherium* and *Holoclemensia* are "neither marsupials nor placentals but represent a separate line of evolution." The toothless mandible, PM 593, he believed, could belong to either genus. The focus on molars may have diverted Butler's attention from the diagnostic incisive alveoli of the edentulous PM 593. In any case, Butler solved his problem by referring the mandible to a new infraclass he named Tribotheria for containing mammals with tribosphenic molars not classifiable as either Metatheria or Eutheria. Turnbull (1971) had already proposed the ordinal name Tribosphina for the same therian groups. In the light of present knowledge both terms can be consigned to the waste basket they were intended to serve.

Forging onward, Aplin & Archer (1987, pp. xxi, xxvli, see also Archer 1984, p. 595) proposed the "supercohort" Protodelphia to contain *Holoclemensia* as a "didelphian," yet not a marsupial!

Still more ambiguous and contradictory opinions regarding the systematic position of each of the two genera described by Slaughter (1965) have been expressed.

The bypassed Albian mandible, the oldest known marsupial and so obviously a marmosid-like didelphoid, is described herewith.

***Adinodon*, new genus (subfamily Adinodontinae, family Marmosidae)**

Type species. *Adinodon pattersoni*, new species.

Included species: The type species only.

Diagnosis. The characters of the genus are those of its genotype. The descriptions that follow apply to both taxa. Size as in small Marmosinae such as *Gracilinanus* or *Marmosa*; dental formula as in didelphoids; alveolus of  $i_3$  staggered; canine alveolus large; superior outline of premolar alveoli ovoid; ramus slender, ventral margin nearly straight.

Age. Albian, late Early Cretaceous.

Etymology. *Adinos* (Greek) crowded, combined with *odontos* (Greek) tooth, in allusion to the crowded lower incisors with  $i_3$  staggered, a didelphoid autapomorphy.

Comparisons. The mandible of *Adinodon* is comparable in size and form to those of such living marmosids as the slightly larger *Marmosa* (fig. 6) Gray, the smaller *Gracilinanus* Gardner & Creighton, and by no particular criteria except dental size and association to the sympatric *Holoclemensia* Slaughter and *Pappotherium* Slaughter each described from upper molars. The nearly complete mandible of the Albian *Kokopellia* Cifelli of the Cedar Creek Formation, Utah, is much larger.

***Adinodon pattersoni*, new species**

Holotype. Fragment of edentulous left mandibular ramus with alveoli of 4 incisors ( $i_2$ - $i_5$ ), canine, premolars ( $pm_1$ - $pm_3$ ) and first molar ( $m_2$ ), Field Museum no. PM 583; collected between 1950–1952, but likely 1950, by Bryan Patterson.

Type locality. Triconodont Gulley, 21/2 miles SW Greenwood Canyon, Forestburg, Montague County, Texas.

Age. Trinity Sand, Paluxy Formation, Albian age, upper Early Cretaceous (Patterson, 1951, but see Winkler, Murray & Jacobs, 1990, p. 99).

Etymology. The species is named in honor of the late Professor Bryan Patterson, long-time curator of the Field Museum's Division of Vertebrate Paleontology, discoverer and describer without naming the oldest didelphoid known to science.

Description of holotype. Mandible slender with alveoli intact except anterior margin of first incisor ( $i_2$ ) and posterior margin of numerical first molar ( $m_2$ ) (fig. 9); alveoli of incisors crowded, that of  $i_3$  (numerical second) wedged between alveoli of phylogenetic  $i_2$  and  $i_4$ , the socket with bony buccal buttress; alveolus of canine large, subrectangular in outline; premolar alveoli ovate, long diameter of each increasing from first to last; alveolar surface length of  $pm_3$  slightly more than combined alveolar surface length of  $i_4$ - $i_5$  (Table 1).

Comparisons with marmosids of all ages indicate that the holotype was a young adult.

The original description of the mandibular fragment PM 583, by Patterson (1956, p. 25, figs 10, 11) follows, "There were clearly four incisors in this specimen (fig. 9). The alveolus of the first [ $i_2$ ] is the smallest of the series and that of the third [ $i_4$ ] the largest, the second and fourth being intermediate in, and of approximately the same size. Relative to the alveoli of the other teeth, that of the canine is enormous. It is elongate-oval in outline and the tooth itself was single-rooted. The eight postcanine alveoli are nearly circular in outline, approximately equal in size, and evidently housed four two-rooted teeth. These are tentatively identified as premolars, the reasons being: (1) the decided break in size and structure between the premolar and molar series should surely be reflected in the alveolar structure, whereas these alveoli are all approximately equal in size; (2) none of the lower molars thus far recovered could have fitted into them.

“Immersion in oil of anise has revealed nearly all the details of the alveoli (fig. 11). That of the first incisor is very procumbent, the remainder becoming progressively more upright in position. The first and second taper evenly to a pointed extremity, the third is longer with a slightly bulbous expansion at the base, and the fourth is the shortest of the series, tapering but little and having a blunt termination. The alveolus for the canine extends ventrally for almost the entire depth of the ramus, tapers only slightly and curves posteriorly to terminate bluntly beneath P<sub>1</sub>. The postcanine alveoli have slightly bulbous terminal expansion, similar to but larger than that seen in I<sub>3</sub> [14]. The alveoli of P<sub>1</sub> are somewhat shorter than those of P<sub>2-4</sub> [= pm<sub>2,3</sub>, m<sub>1</sub>], which extend ventrally for slightly over half the depth of the ramus.

“The horizontal ramus, so far as preserved, is slender throughout, except in the region of the canine, where it is decidedly swollen on the external side. The ventral border is straight from the canine posteriorward, and slightly concave beneath the incisors. A mental foramen is present below the anterior extremity of P<sub>2</sub>. The ligamentous symphysis extends back to a point beneath P<sub>1</sub>. No trace of an internal mandibular groove can be seen.”

Patterson was undecided regarding the systematic position of the mandibular fragment whether metatherian, eutherian or neither. He (1956, p. 29) opted for neither. “The four incisors,” in his opinion, “suggest pantotherian or metatherian affinities, the supposed four premolars pantotherian or eutherian. The molars definitely exclude the Forestburg forms from the Order Pantotheria. The incisor and premolar formulae and the molar structure present a combination such as must have occurred in the placentalmarsupial ancestry.” Because of his misappraisal of the premolar number, uncritical appreciation of the incisor morphology, neglect to compare the specimen with small didelphids including one with a deciduous m<sub>1</sub>, and disregard of the staggered condition of i<sub>3</sub>, Patterson failed to realize that his specimen had already attained metatherian grade.

Remarks. My illustration (fig. 9) of the incisor field with alveoli cleared by immersion in oil of anise, differs somewhat from that of Patterson’s (1956, fig. 11, reproduced here in fig. 9) because of a slight inward tipping of the mandible. The altered position shows the proximal or basal portion of the first alveolus (i<sub>2</sub>) nearer the base of the third alveolus (i<sub>4</sub>), and the second alveolus (i<sub>3</sub>) slightly deeper than in Patterson’s figure. More significantly, the basal third of the second alveolus (i<sub>3</sub>) is wedged between and slightly behind the first and third alveoli, its superior border higher, less concave than that of either the second or fourth alveolus. In short, the didelphoid dental formula, mandibular size and form and the staggered alveolus of i<sub>3</sub> are, in combination, unequivocal evidence of didelphoid presence in Early Cretaceous.

Table 1: Mandibular measurements of four marsupial species. The measurements of all four taxa are based on condition of mandible of *Adinodon*. The new genus and *Gracilinanus* are nearly the same size. *Marmosa* and *Kokopelia* are larger and nearly the same size as each other but dentally are different. Comparisons of teeth, however, are outside the scope of this paper.

	<i>Adinodon</i> <i>pattersoni</i> <sup>1)</sup>	<i>Gracilinanus</i> <i>agilis</i> <sup>2)</sup>	<i>Marmosa</i> <i>murina</i> <sup>3)</sup>	<i>Kokopellia</i> <i>juddi</i> <sup>4)</sup>
Total length i <sub>2</sub> —m <sub>2</sub>	8.39	5.88	8.56	7.94
Total length i <sub>3</sub> -ascending ramus	—	10.65	13.21	15.90
Total length i <sub>2</sub> -condyle	—	17.24	19.34	—
Mandibular height at m <sub>2</sub>	1.98	2.05	2.61	3.28
Mandibular height at C	1.49	1.21	1.98	1.83
Pm <sub>1</sub> , greatest alveolar length	1.01	1.05	1.25	1.02
Pm <sub>2</sub> , greatest alveolar length	1.03	1.08	1.43	1.26
Pm <sub>3</sub> , greatest alveolar length	1.10	0.94	1.40	1.99
Pm <sub>1-3</sub> , greatest alveolar length	3.34	3.49	5.25	4.56
C alveolar length	1.64	1.13	1.89	1.65
M <sub>2-5</sub> alveolar length	—	5.63	7.48	7.95

<sup>1)</sup> Albian (lower Cretaceous) Texas, <sup>2)</sup> Bolivia (Recent), <sup>3)</sup> Suriname (Recent), <sup>4)</sup> Albian (lower Cretaceous) Utah

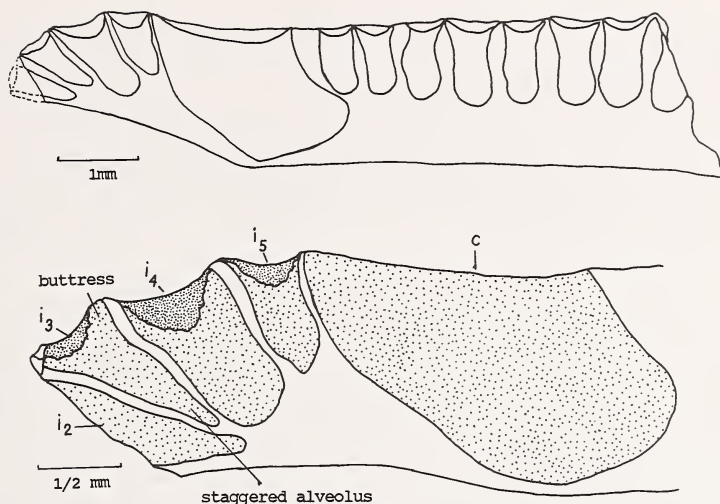


Fig. 9: *Adinodon pattersoni* (holotype). Fragment of left ramus cleared with oil of anise for revealing alveolar outlines. Upper, buccal surface of fragment (i2-5, c, pm1-3, m2), copied from Patterson (1950); same specimen i2-c only seen from labial surface tilted slightly inward to reveal full depth of staggered alveolus i3. Redrawn from Hershkovitz (1982).

Comparisons. The edentulous mandibular fragment differs more or less from similar species of the family Marmosidae, by more slender nearly parallel dorsoventrally-sided ramus; canine larger than that of any didelphoid with comparably sized mandible and of the same-aged *Kokopellia juddi* with normal size canine. Measurements were not included with the original description of *Kokopellia juddi* and those given in table 1 are from a much worn cast kindly donated by Dr. Richard Cifelli. Part of the originally published diagnostic characters from Cifelli (1993, p. 9443) follows.

“Similar to Cretaceous Marsupialia in postcanine dental formula and in general morphology of lower teeth but differs from all described genera in having posteriorly (rather than lingually) placed hypoconulid. Molar morphology differs from primitive tribotheres (e. g., *Kermackia*) in having relatively broader talonids and in lacking a distal metacristid; from advanced tribotheres (e. g., *Iugomortiferum*) in having a more lingually situated paraconid and stronger labial postcingulid; and from early Eutheria (e. g., *Prokennalestes*) in dental formula, presence of a labial postcingulid, lesser development (or lack) of accessory cusps on the ultimate lower premolar, and the presence of an unreduced, more lingually situated paraconid.”

The North American Late Cretaceous *Eodelphis* Matthew, with genotype and only known species, *E. browni*, is marmosine-like in size, proportions and staggered i3 but somewhat larger than the holotype of *Adinodon pattersoni*, with slightly heavier mandible. The lower incisors, according to Matthew (1916, p. 483) are 3 in number, “the second somewhat enlarged, others minute, crowded, vestigial.” The staggered i3 is evident in the illustrations (Matthew 1916, fig. p. 486; pl. 2), the same photographs

reveal the position of the expected fourth incisor ( $i_4$ ) as a minute alveolus wedged between  $i_4$  and  $c$ . Reig, Kirsch & Marshall (1987, p. 81) have identified *Eodelphis* as a genus of the family Stagodontidae.

Upper molars of the *Marmosa*-size *Holoclemensia texana* Slaughter and the referred lower molar of the paratype, are the same age and from the same formation as *Adinodon pattersoni* and combine all marsupial diagnostic dental characters. No living didelphoid, however, displays the same combination of characters whether of upper or lower molars. Absence of stylar cusp C is problematic. Slaughter (1971) believed that the metacone smaller than the paracone of *Holoclemensia* was uncharacteristic of marsupials but it was presumed that enlargement evolved with time. The metacone is indeed larger than the paracone in *Marmosa* and all other marmosids and didelphids, but is variable in the didelphoid Caluromyinae. Because of the disparity direct comparison between *Holoclemensia* and *Adinodon* is impossible except for estimates of probable body size. It is remotely possible, nevertheless, that the holotypes of *Holoclemensia* and *Adinodon* might represent one and the same genus, but because of sympatry not the same species. Marshall et al. (1990, p. 484) classify *Holoclemensia* as a stagadontid (order Sparassodonta), a questionable assignment.

*Marmosopsis* from the Brazilian Itaboraí Formation (Middle Paleocene) was described by Paula Couto (1962, p. 157) as a didelphid almost indistinguishable from living *Marmosa* (fig. 6). The description was based on a mandible lacking incisors, canine and  $pm_1$ . Abundant additional material consisted of fragments of right and left mandibles with more than enough teeth to complete the molar formula. Paula Couto (1962, p. 157) confessed doubt, however, that a living genus such as *Marmosa* could have survived from Paleocene to present without marked differentiation. Nevertheless, time lapse and some trivial dental differences seemed adequate for separation of *Marmosopsis* from *Marmosa*. Rationalization for the separation of *Adinodon* from *Marmosa* or other living marmosids is based on the knowledge that between Early Cretaceous or between any past epoch and present, mouse opossums of the family Marmosidae have evolved. They have been reclassified as 5 subfamilies and those of the subfamily Marmosinae rearranged from one to four genera. The taxa are distinguishable interse primarily by other than mandibular and alveolar characters.

Metatherian-eutherian grade. Indecision regarding the affinities of PM 583 and associated taxa induced Patterson (1956, p. 13) to categorize them as of "metatherian-eutherian grade" meaning perhaps that they had not attained the evolutionary grade of either clade. In no sense could "metatherian-eutherian grade" mean ancestral, intermediate, hybrid, or anything meaningful. Nevertheless, "metatherian-eutherian grade" has since acquired a pseudoequivalence to subclass (cf. Clemens et al. 1979, p. 9; Kielan-Jaworowska et al. 1979, p. 182, etc.) for taxa that should be categorized as *incertae sedis*, or assigned to an existing or specially formulated hierarchy. In this particular case, size and proportion of the fossil, mandibular dental formula, and the telltale staggered alveolar  $i_3$  mean didelphoid, most likely marmosid.

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### Zusammenfassung

In der Evolution der Marsupialia ging eine fortschreitende Reduktion der Schnauzenlänge einher mit Zahnstauchung und Zahnverlust. Dem Verschwinden des ersten unteren Schneidezahnes bei den frühesten Beuteltieren folgte die Rückbildung und der Verlust von ersten Molaren, den sogenannten „Milchprämolaren“, vermutlich in der frühen Kreide oder im späten Jura. Stauchung und Herausschieben des dritten unteren Schneidezahnes erfolgten nicht später als in der frühen Kreidezeit und bildeten das entscheidende Merkmal der Kohorte Didelphimorphia. Die phylogenetische und biogeographische Bedeutung des herausgehobenen und gewöhnlich buccal von einem Knochenwulst abgestützten  $i_3$  (numerisch der zweite) wird diskutiert. Die Zahnformeln der Metatheria und der Eutheria werden verglichen, und es wird gezeigt, daß sie entwicklungsbiologisch und in der Abfolge der Zähne nicht homolog sind. Eine in dieser Arbeit beschriebene neue Gattung und Art aus dem Albian von Texas (obere Unterkreide) repräsentiert wahrscheinlich das älteste bekannte didelphoide Beuteltier. Sein herausgehobener  $i_3$  impliziert eine Differenzierung der Metatheria in der frühen Kreide oder im späten Jura.

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